Review Article

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The egg-laying behaviours of the gastropod *mollusks*

Abstract

The gastropods are commonly known as snails and slugs. They are a large taxonomic class within the phylum *Mollusca*. The cerebral neurosecretory caudodorsal cells (CDCS) of the fresh water pulmonate *Lymnaea* control egg laying, an event that involves a pattern of stereotyped behavior. The CDCS synthesize and release multiple peptides, among which is the ovulation hormone (CDCS). It is thought that each peptide controls a specific aspect of the processes involved in egg laying. Dopamine is commonly found in the molluscan central nervous system (CNS). In some gastropods, dopamine has been implicated in the regulation of egg laying behavior that stimulates protein secretion from albumen gland. The albumen gland in *pulmonate* snails is an accessory gland of the female reproductive tract. It synthesizes and secretes perivitelline fluid (PVF), which is composed mainly of proteins and polysaccharides.

Keywords: CDCS, dopamine, peptides, CDCH

Volume 4 Issue 2 - 2018

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Received: January 24, 2018 | **Published:** March 07, 2018

Abbreviations: CDCS, caudodorsal cells; CNS, central nervous system; PVF, perivitelline fluid; CDCH, caudodorsal cell hormone

Introduction

Mollusca is the largest marine, phylum about 23% of all the named marine organism.[1] The gastropods, more commonly known as snails and slugs, are a large taxonomic class within the phylum *Mollusca* according for 80% of total *mollusca*.[2] Fresh water gastropods are divided in to two subclasses, *Prosobranchia* and *Pulmonata*. Most of the species associated as intermediate hosts of helminthes parasite.[3,4] *Planorbidae* and *Limnaedae* colonized in freshwater habitat because they have broad physiological and ecological concepts. The anatomy, behavior, feeding, and reproductive adaptations of gastropods vary significantly from one clade or group to another. Therefore, it is difficult to state many generalities for all gastropods. Observation showed that the snail population and frequency of infection greatly varies from place to place and seasonally. The snail has to respond against environmental change. The first review of reproduction in fresh water pulmonates are pointed by Duncan[5] later on Geraets & Joose.[6] Among pulmonates hermaphroditism is universal and almost universal among ophisthobranche gastropods but rare in all other gastropods.[7] The hermaphroditism means adult has both female and male functioning system but it is not necessary that individual engages both sexual function in any single mating.[7] Aquatic gastropods generally deposite their eggs in gelatinous capsule that are attached to surface or aquatic plant leaves. The self fertilization in pulmonates was first noted by.[8] The gonad is called ovotestis/ gonadal tissue and sperm are passed through via duct in to vesicular seminal. The release of ova from the gonads is controlled by hormone at least in the ophisthobranch and basometophoran pulmonates and may be land snail.[7] The endocrine gland secrete these hormone have been characterized in *Lymnaea* and *Aplysia*.[7] The caudodorsal cells are present in cerebral ganglion and release two ovulation hormone. Abiotic factors increases the rate of reproductive capacity.[9] Srivastava et al.[10] reported significant positive correlation between acetyl cholinesterase and egg laying in *Lymnaea acuminata* a fresh water pulmonates. The aim of the present review is demonstrate the role CDCs cells, their structure and mechanism involve in reproduction behavior of pulmonates.

Role of caudo dorsal cells (CDCs)

Roubos et al.[11] reported that in gastropod the peptidergic neurons controlling egg-laying produce multiple peptides which are cleaved from a common precursor. Before egg laying, these cells produce a discharge of action potentials during which the peptides are released and egg-laying behaviour is initiated.[12] Hermann et al.[13] reported that in *Lymnaea stagnalis* the neuroendocrine cells controlling egg-laying are the caudodorsal cells (CDCs) which is a group of about 100 electrotonically coupled neurones, located in the cerebral ganglia. These cells have axons that form a neuro haemal area in the cerebral commissure and from this area, CDC peptides are released into the blood during the electrical CDC discharge.[14] The CDCs exhibit three states of excitability, resting, active and inhibited each with distinct electrophysiological characteristics. Transitions between these states can occur spontaneously or can be induced experimentally.[13] When the CDCs are in the resting state, a train of depolarizing current pulses elicits an after discharge, the active state. From this active state, the cells enter the inhibited state.[15] The ability to generate discharges is positively correlated with the amplitude of the depolarizing after potential that is induced by a short train of depolarizing current pulses.[16] In the isolated central nervous system, a CDC discharge can be elicited by repetitive supra threshold depolarization of resting-state CDCs.[17] Egg-laying behaviour is a sequence of stereotyped movements in which three phases can be distinguished: resting, turning and oviposition.[11] During turning, the animals make long-lasting turns of their shell through more than 60° relative to the head-foot. These turns only occur in the second phase of egg-laying and are not part of the animal's other behavior patterns.[18] It is to be expected, therefore, that the motor neurones involved in these shell movements will be inhibited during the resting phase and excited during the turning phase of egg-laying behavior.[19] In *Aplysia*, it has been demonstrated that peptides released by the bag cells during and after discharge have a number of effects on the electrical activity of central neurons *in vitro*.[20] These peptides also affect gill and siphon contractions and the

arterial system. Injections of these peptides into intact animals also induce behavioral changes.[13] An injection of CDCH (the ovulation hormone) induces egg-laying in *Lymnaea* although, following such injections, the animals do not show the first phase of egg-laying behaviour.[14] Alpha CDCP and CDCH have an auto-excitatory function in *Lymnaea*.[15] Until now; it has not been possible to study the role of the CDC peptides in regulating the neurones involved in overt egg-laying behaviour. With the identification of the nerves and motor neurones involved in turning behaviour during egg-laying in *Lymnaea*, we now have a neuronal model that may allow us to determine the effects of the peptides released by the caudodorsal cells during egg-laying.[19] The central nervous system of the freshwater pulmonate snail *Lymnaea stagnalis* contains several neurosecretory cells which differ in histochemical and ultrastructural characteristics and are often found in groups which occur at characteristic locations in the ganglion ring.[21] The axons of the neurosecretory cells run to the periphery of nerves, commissures or connectives where they terminate with many neurohaemal endings which release the products into the haemolymph by exocytosis.[11] The caudo-dorsal cells (CDC), located in the cerebral ganglia, constitute one of these groups, and produce an ovulation hormone.[22] Cells producing ovulation hormone are also known in opisthobranchs: the 'bag cells' of *Aplysia* which are usually electrically silent.[23] The peptidergic Caudodorsal Cells (CDC) of the freshwater snail *Lymnaea* stagnalis control egg laying and egg-laying behaviour by releasing various peptides that act upon different targets.[22] Egg laying lasts about 2 hours and involves ovulation of up to 200 oocytes from the ovotestis, packaging of these cells by various types of female accessory sex gland into an egg mass, and oviposition. Kandel[24] argues that the bag cells of *Aplysia* have a 'triggering' function in the all or none act of egg-laying. Also usually silent, these cells can respond to strong electrical shock to the connectives with an after discharge in which all cells participate and during which the hormone is released. Vlieger et al.,[25] reported that a major factor determining the massive discharge of the bag cells is electrotonic coupling by 'remote' axonal processes. He also observed that in *L. stagnalis* electrotonic coupling appeared to be quite pronounced between all CDC and could very well explain that excitation in one cell spreads to all others, especially since in active cells there is a progressive increase in spike width, facilitating transmission across the junctions. Curti et al.[26] reported that the importance of electrical coupling is underlined by the results on the morphology of the CDCs.

Structure of the CDCs

Roubos et al.[27] reported that the CDC occur in two clusters in the cerebral ganglia (left: 25 cells, right: 75cells). Each cluster contains 7 ventral CDC that have an axon branch running through the cerebral commissure. The "crossing axons" make electrotonic contacts with the contra lateral CDC, thereby enabling the cells of both clusters to function as one unit.[28] Smirle et al.[29] reported that the CDC are characterized by a well developed rough endoplasmic reticulum (RER) and Golgi apparatus and by electron-dense secretary granules with a mean diameter of about 150 nm. Roubos et al.[11] reported that the granule contents, including the ovulation-inducing peptide Caudodorsal Cell Hormone (CDCH), are released into the haemolymph by exocytosis from neurohaemal axon terminals located in the periphery of the cerebral commissure. Furthermore, secretion occurs into the intercellular space of the central nervous system, from nonsynaptic release sites in the cerebral commissure.

Role of dopamine

Dopamine is commonly found in the molluscan central nervous system (CNS). In gastropods, dopamine has been implicated in the regulation of egg laying behaviour in *L. stagnalis*.[18] Bislimi[30] shown that the PVF secretion by the albumen gland could be stimulated by forskolin, cAMP, brain extract and dopamine. Dopaminergic neurons have been localized in the CNS of some snails such as *L. stagnalis*, *Helix pomatia*, *Aplysia californica* and *Planorbis corneus*, and they were mapped in the buccal ganglia of *Helisoma trivolvis*. Morgan[31] showed that 3H-dopamine accumulates specifically in the buccal, cerebral, pedal, left parietal and visceral ganglia, and the left pedal ganglion contains a greater amount of dopamine than the right. Kiehn et al.[32] identified a giant dopaminergic neuron in the left pedal ganglion in the CNS of *H. trivolvis* containing neurons in the albumen gland and carrefour they neither specified the type of catecholamines nor their distribution within the albumen gland and the carrefour. Pena & Edema[33] have shown that dopamine stimulates protein secretion from albumen gland. The albumen gland in pulmonate snails is an accessory gland of the female reproductive tract. It synthesizes and secretes perivitelline fluid (PVF), which is composed mainly of proteins and polysaccharides. Kiehn et al.[32] reported that mature oocytes are released by the ovotestis and travelvia the hermaphroditic duct into the carrefour, where the albumen gland duct empties. In the carrefour the eggs are fertilized and then are coated with the PVF. The importance of the PVF lies in the fact that it is a major nutrients source for the developing embryo since the oocytes themselves contain very little vitellogenic protein. Mukai[34] reported that the secretion of the PVF and the arrival of oocytes at the carrefour must be synchronized, suggesting a precise control of the PVF release. Kiehn et al.[32] identified a neuronal plexus in the duct of the albumen gland and the carrefour, which suggested that a nervous mechanism may be involved in the control of the PVF release. Furthermore, catecholamine-containing axons were identified in the albumen gland, carrefour and some other reproductive organs of *L. stagnalis* and other species of pulmonate snails. Bain et al.[35] observed that overt egg laying behaviour consists of a number of stereotyped behavioural acts. It begins with cessation of locomotion and posture changes. After about one hour the animal starts crawling about and cleans the substrate by rasping with its buccal mass before depositing the egg capsule. Actual oviposition takes 10-20 minutes depending on the size of the egg mass.[35] Finally, the animal crawls back along the egg mass, touching it with the lip, before moving off.

Role of environmental factors

Srivastava & Singh[18] noted that temperature increases beyond 33ºC the reproductive rate decline. Sudden drops in temperature promote egg mass abortion.[36] A temperature of 25ºC is considered for optimal for oviposition and growth in *pomacean* snails[37] Earlier study has shown that decrease in temperature from 20ºC to 8ºC stopped the oviposition of snail *Lymnaea stagnalis*, because of reduction in activities of neurosecretory caudo dorsal cells (CDCs).[38] Srivastava et al.[10] reported that the fecundity, hatchability and survival of young snails show positive correlation with temperature. Seasonal fluctuations in the secretary neuro endocrine cells of *Aplysia californica* inhibited the protein Kinase A and C which play a significant role in regulation of egg laying hormone.[39] According to their cAMP and diacylglycerol second messenger pathways are regulated on a seasonal basis.[40] Abiotic factors of the environment vary from one

Citation: Srivastava AK, Singh VK. The egg-laying behaviours of the gastropod *mollusks*. *Adv Tissue Eng Regen Med Open Access.* 2018;4(2):21–25.
DOI: 10.15406/atroa.2018.04.00072

season to other.[41] The aquatic environment has numerous physical and chemical parameters that may influence the physiology of fresh water organism.[42] Embryological development is highly influenced by the change of ecological factors in aquatic environment.[9] Ranjan[43] stated that breeding season and the incubation period vary with the nature of the environment. Raut[44] concluded that the rate of breeding in the number of snail's viz., *Lymnaea acuminata*, *Indoplanorbis exustus* and *Acrostoma variabilis* were governed by temperature, rainfall and food. Temperature negatively influenced the incubation period that means they reduced the incubation period and enhanced hatchability of snails.[45] Possibly due to high temperature, low intake of oxygen concentration in water and increase in CO_2 concentration and low pH of water. Seasonal variations were reported in mussel Camp contents[46] were mainly observed in the mantle, reflecting a relationship with the gametogenesis cycle.[47] Besides temperature, also other environmental and nutrition condition influence gametogenesis and spawning[48] and a relationship with cAMP levels in the mantle was recently evidenced by Blanco et al.[49] Indeed, high cAMP levels were found in autumn and winter, in parallel with lowest levels of ATP, ADP and AMP, possibly related to the activation of glycogen degradation to fuel gonadal development.[48] The process of cellular growth and divisions requires the synthesis of nucleic acids and protein. Increase in pH from 7-8 caused a significant increase in DNA and protein level in ovotestis of *L. acuminata*.[36] Dissolved oxygen is one of the most important ecological factors for survival of snail and other aquatic life. In general, most pond water can hold about 10 to 12 mg/l of oxygen. Temperature is one of the most important factor affecting dissolved oxygen levels. Oxygen dissolves easier in cold water than warm water. As temperature increases oxygen level decreases. Critically, low oxygen levels can occur during, hot summer months, when capacity is decreases due to high temperature and organism have a higher demand. In winter season water holds more oxygen than summer season. Different classes of gastropods show variation in oxygen consumption such as prosobranch and pulmonate snails have similar levels of oxygen consumption whereas, ophisthobranch snails have higher oxygen consumption. *Lymnaea* is very sensitive to dissolved oxygen content of water. It has been reported that fecundity in some animal does not respond to higher oxygen. It has also been reported that dissolved oxygen below 20% saturation causes stress to fresh water muscles. High oxygen concentration changes the chemical composition of water as well as morphological characteristics of caudo dorsal cells (CDCS) and physiology of snails.[40] Dissolved oxygen increased the incubation period and the hatchability through incomplete or slow development of the embryo. These hydrogen ions determine the acidity of the aquatic body, accounting the change in pH. Carbon dioxide decreases the pH of water because of increase in concentration of H+. The direct effect of high CO_2 exposure can be reduction in metabolism, protein synthesis, growth rate and reproduction in marine animals.[50]

Role of AChE enzyme

Srivastava et al.[10] reported that a significant positive correlation between the AChE activity and the fecundity of snail. The enzyme is responsible for the breakdown of ACh in cholinergic synapses, preventing continuous nerve firing, which is vital for normal cellular neurotransmitter functioning.[48] It indicates that the reproductive capacity of snail up to some extent is mediated through cholinergic stimuli in the brain of snail. Singh et al.[51] reported that prostaglandins have significant role in the egg laying of snail *L. acuminata* and after treatment with molluscicides it inhibit the prostaglandins metabolism in exposed snail. The AChE inhibition result in accumulation of acetylcholinesterase at the nerve synapses so that the post synaptic membrane is in a state of permanent stimulation producing paralysis, ataxia and general lack of coordination in neuromuscular system and eventual death of the snails.

Conclusion

Present review summarizes that the how egg laying affected by abiotic factors and functioning of the neural cell enzymes. Because Molluscs are still used extensively as model species for neuro-endocrine processes that regulate different types of behaviors. Regulation of egg laying behaviors for understanding the evolution of hermaphroditic mode of reproduction.

Acknowledgements

None.

Conflict of interest

There are no financial conflicts of interest to report.

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Citation: Srivastava AK, Singh VK. The egg-laying behaviours of the gastropod *mollusks. Adv Tissue Eng Regen Med Open Access.* 2018;4(2):21–25.
DOI: 10.15406/atroa.2018.04.00072